To what extent can we predict variation of bryophyte and tracheophyte community composition at fine spatial scale along an elevation gradient?

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HIGHLIGHTS

GRAPHICAL ABSTRACT. DISTRIBUTION OF 413 2 ×2 M PLOTS IN THE WESTERN SWISS ALPS (A). IN THIS AREA, WE TESTED OUR CAPACITY TO EXPLAIN SPECIES COMPOSITION (PRESENCE/ABSENCE) OF TWO PLANT LINEAGES (BRYOPHYTES AND TRACHEOPHYTES) USING CLIMATIC (E.G., ARIDITY, SNOW COVER, PRECIPITATION AND TEMPERATURE) AND OTHER ENVIRONMENTAL VARIABLES (E.G., CANOPY HEIGHT, SOIL PH, SLOPE AND REMOTE SENSING DATA) AT 2–25 M RESOLUTION, SPATIAL FACTORS, AND THE COMPOSITION AND ARCHITECTURAL TYPES OF THE OTHER LINEAGE. ARROW THICKNESS IS PROPORTIONAL TO THE PERCENT VARIANCE OF COMMUNITY COMPOSITION OF ONE LINEAGE EXPLAINED BY SPECIES COMPOSITION AND ARCHITECTURE OF THE OTHER LINEAGE, CLIMATIC AND OTHER ABIOTIC VARIABLES (B). TRACHEOPHYTE COMPOSITION WAS THE BEST PREDICTOR OF BRYOPHYTE COMPOSITION, REFLECTING BOTH DIRECT INTERACTIONS AND UNMEASURED (HIDDEN) ENVIRONMENTAL FACTORS. THE TOTAL EXPLAINED VARIANCE AND ASSOCIATED DRIVERS SUBSTANTIALLY VARIED WITH ELEVATION, UNDERLINING THE FACT THAT THE STRENGTH OF THE SPECIES COMPOSITION-ENVIRONMENT RELATIONSHIP VARIES DEPENDING ON ENVIRONMENTAL CONDITIONS (C)

- 25 m-resolution climate data played a minor role in explaining mountain plant composition.
- Tracheophyte composition was the best predictor of bryophyte composition.
- The strength of the species composition-environment relationship varied with elevation.
- Spatial effects and vegetation architecture played a key role in alpine environments.
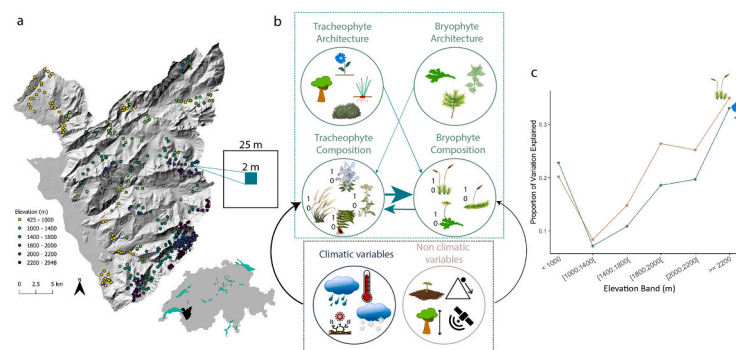
ABSTRACT

Mounting evidence points to the need for high-resolution climatic data in biodiversity analyses under global change. As we move to finer resolution, other factors than climate, including other abiotic variables and biotic interactions play, however, an increasing role, raising the question of our ability to predict community composition at fine scales. Focusing on two lineages of land plants, bryophytes and tracheophytes, we determine the relative contribution of climatic, non-climatic environmental drivers, spatial effects, community architecture and composition of one lineage to predict community composition of the other lineage, and how our ability to predict community composition varies along an elevation gradient. The relationship between community composition of one lineage and 68 environmental variables at 2-25 m spatial resolution, architecture and composition of the other lineage, and spatial factors, was investigated by hierarchical and variance partitioning across 413 2x2m plots in the Swiss Alps. Climatic data, although significant, contributed less to the model than any other variable considered. Community composition of one lineage, reflecting both direct interactions and unmeasured (hidden) abiotic factors, was the best predictor of community composition of the other lineage. Total explained variance substantially varied with elevation, underlining the fact that the strength of the species composition-environment relationship varies depending on environmental conditions. Total variance explained increased towards high elevation up to 50 %, with an increasing importance of spatial effects and vegetation architecture, pointing to increasing positive interactions and aggregated species distribution patterns in alpine environments. In tracheophytes, an increase of the contribution of non-climatic environmental factors was also observed at high elevation, in line with the hypothesis of a stronger environmental control under harsher conditions. Further improvements of our ability to predict changes in plant community composition may involve the implementation of historical variables and higher-resolution climatic data to better describe the microhabitat conditions actually experienced by organisms.

1. Introduction

The increasing availability of species distribution data and climatic conditions worldwide at resolutions up to 1 km^2 has fueled a growing body of literature on the impact of global change on biodiversity (Lembrechts et al., 2020). The climatic conditions described in widely used climatic databases, such as Chelsa (Karger et al., 2017) and Worldclim (Fick and Hijmans, 2017), characterise long-term average atmospheric conditions from interpolated measures at standardised weather stations, whose sensors are typically located at ~2 m above a mown lawn and characterise free-air (macroclimatic) conditions. Mounting evidence increasingly reveals, however, large differences between such macroclimatic conditions and the conditions actually experienced by organisms (microclimates) due to local variations driven by topography, wind and vegetation (Lembrechts, 2023). Differences between macro- and microclimate are expected to increase in response to increasing differences in elevation and topography. In mountain regions in particular, microclimate can vary noticeably over very short distances (Dobrowski, 2011; Dobrowski et al., 2009; Graae et al., 2018; Lembrechts et al., 2019), with substantial consequences for our ability to predict climate change impacts (Patiño et al., 2023; Scherrer et al., 2011). Scherrer et al. (2011) reported for instance a six-fold increase of the predicted habitat loss under a scenario of 2 K increase when shifting from a spatial resolution of 1 m to 100 m. Ignoring this variability has led to conflicting predictions of climate change impacts on species distributions (Lembrechts, 2023; Maclean and Early, 2023; Randin et al., 2009). To fully understand and better predict how biodiversity relates to climate and its changes, finer-scale climate data need to be integrated into ecological research (Lembrechts et al., 2019; Maclean and Early, 2023).

The issue of geographic scale and associated climatic data is intimately associated with the size of the organisms (Pincebourde and Woods, 2012). A large species requires a relatively large 'physical space', which often translates into a larger environmental niche (Morse, 1974). Any tall structure such as a tree is aerodynamically coupled to the atmosphere (Körner and Hiltbrunner, 2021). Its niche may hence be best described by environmental factors at a coarser resolution than that of smaller species, occupying smaller physical spaces that differ from each other in terms of microhabitats (Pincebourde and Woods, 2012). Microenvironmental conditions are modified by the presence of large plants, generating a variety of small physical spaces that only smaller species can occupy (Aarssen et al., 2006). The herbaceous layer plays, for example, an important role in the modulation of the availability of microenvironmental niches for the bryophyte layer. There is a trade-off between the shade provided by herb cover, protecting the underlying moss layer from desiccation, and the negative impacts due to dense herbaceous layers and associated litter (Bergauer et al., 2022; Malmer et al., 2003). On the other hand, bryophytes can facilitate seed retention, maintain high moisture levels, stabilise soils, and protect seeds and seedlings from consumers (Lett et al., 2018; Gavini et al., 2019). Conversely, a thick moss layer may also hamper seed germination and even compete with forbs (Keizer et al., 1985; Malmer et al., 2003; Zamfir, 2000). Species composition and vegetation structure thus reflect abiotic and biotic factors, and may hence potentially be better predictors of individual species occurrences than abiotic factors alone (Schaffers et al., 2008).

Shifting from coarse to fine scales thus raises the question of the ecological relevance of the variables that operate at a given resolution, and their availability across spatial extents (Bruelheide et al., 2018; Damschen, 2018). Microclimate data at resolutions of tens of centimetres, relevant for small-sized organisms like bryophytes, can be recorded using climatic sensors deployed across microhabitats, but at relatively low spatial extent (about 1 ha, see e.g., Man et al., 2022; Shen et al., 2022). At larger spatial extents, regional climate models, produced by dynamically downscaling earth system model outputs (e.g. by using the latter as boundary conditions and resolving local climate

processes at a higher spatial resolution), provide a complementary approach to generate fine-scaled climate data at a resolution from ten to a few hundreds of metres (Giorgi, 2019). Such data have been increasingly available across regional or even larger spatial extents (e.g., Haesen et al., 2021; Patiño et al., 2023).

As we move to finer resolution, other factors than climate, including local environmental conditions (e.g. soil, land use) and biotic interactions play, however, an increasing role (Gazol and Ibáñez, 2010; Laliberté et al., 2009; Lewis et al., 2014; Pearson and Dawson, 2003; Wisz et al., 2013). Both spatial extent and data resolution may influence the amount of variance observed in a given environmental factor and thus its observed relationship with species composition (Siefert et al., 2012).

Furthermore, the strength of species/environment relationships and their drivers may vary from one environment to another (Paula-Souza & de Paula-Souza and Diniz Filho, 2020). It has, for instance, long been suggested that temperate communities are more environmentally controlled than tropical ones due to stronger abiotic niche constraints in temperate areas (Gálvez et al., 2023; Leibold and Chase, 2017; Myers et al., 2013; Souffreau et al., 2015). Transposing this expectation along an altitudinal gradient, one could therefore hypothesise that the composition of high-elevation communities is under stronger environmental control than that of lowland communities (Klanderud et al., 2015; Pottier et al., 2013). Likewise, the stress gradient hypothesis posits that biotic interactions shift from competition to facilitation under harsh conditions (Soliveres and Maestre, 2014), raising the hypothesis that vegetation architecture plays an increasing role to explain community composition towards high elevation.

In line with previous studies on the assembly of plant communities (D'Amen et al., 2017; Pottier et al., 2013; Scherrer et al., 2019), we took advantage of RechAlp, a platform for transdisciplinary research in the Western Swiss Alps (von Däniken et al., 2014; https://rechalp.unil.ch), which offers an unprecedented biotic and abiotic inventory in a single mountain region, to assess our ability to identify and compare the fine-scale drivers of the composition of two lineages of plants, namely bryophytes and tracheophytes. More precisely, we addressed the following questions: What is the relative contribution of climatic, non-climatic environmental drivers, spatial effects, community architecture and composition of one lineage to predict community composition of the other lineage along a strong elevation gradient? Summing-up the contribution of the above factors, to what extent can we predict the composition of bryophyte and tracheophyte communities, and how does our ability to predict community composition vary with elevation?

2. Material and methods

2.1. Study area

This study took place in the Western Swiss Alps, on an area of approximately 700 km^2 (Fig. 1), for two main reasons. First, elevation ranges between 375 m and 3210 m, generating strong climatic gradients, with average temperature and precipitation ranging from 8 °C and 1200 mm at 600 m to −5 °C and 2600 mm at 3000 m (Randin et al., 2006). Second, a wide range of biotic and abiotic information was already collected in the framework of Rechalp (http://rechalp.unil.ch), a geodatabase of scientific metadata including detailed information on soil, climatic and topographic conditions as well as complete inventories of vascular plant species in 2 × 2 m plots separated from each other by a minimum distance of 200 m to minimise spatial autocorrelation (Dubuis et al., 2011). The survey was limited to open, non-woody vegetation only, including grasslands, meadows, rocks and screes, and followed a random-stratified sampling design based on elevation, slope and aspect (Hirzel and Guisan, 2002).
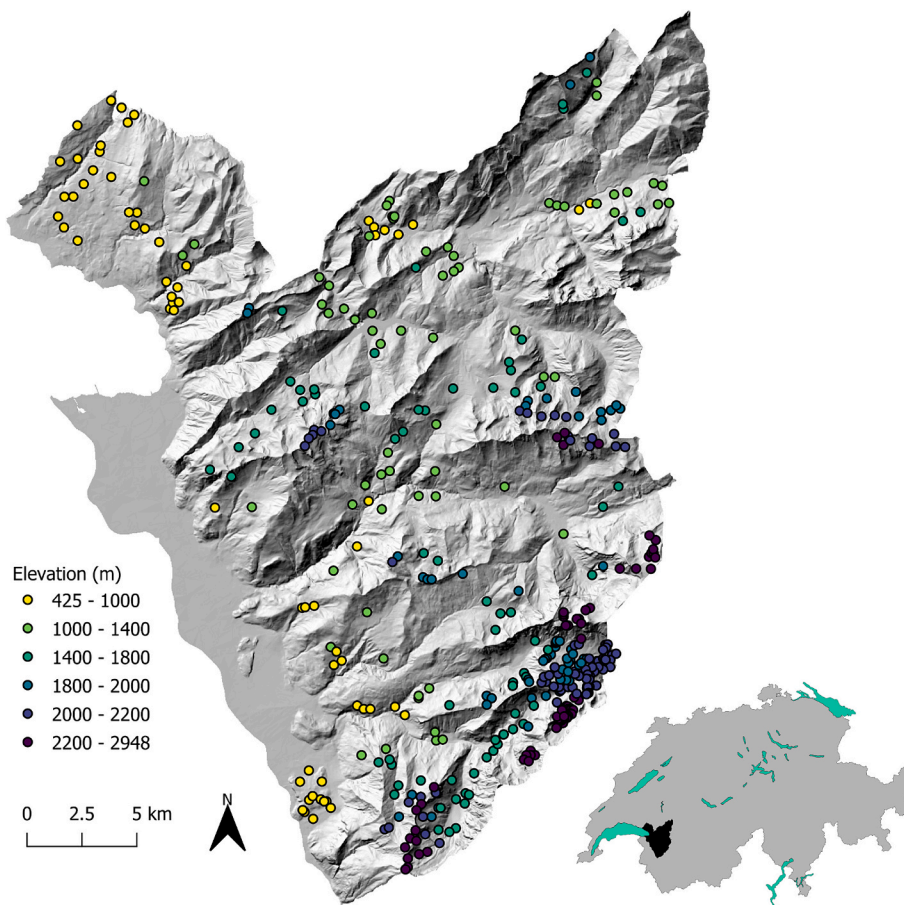
Fig. 1. Study design. Distribution of 413 2 × 2 m plots in the Western Swiss Alps along an elevation gradient.

2.2. Vegetation sampling

Cover data of tracheophytes (nomenclature of Juillerat et al., 2017) was recorded between 2002 and 2022, for 1057 2 × 2 m plots (Buri et al., 2017; Dubuis et al., 2011; Randin et al., 2006).

Complete bryophyte inventories were performed in 413 of these plots (Fig. 1) between 2017 and 2021 by the same team of researchers (FC and AV). These 413 plots were selected to cover the entire study area and elevation gradient, and encompass a similar number of plots within each of six elevational bands (see below). Plots were localized in the field using a GPS Trimble® Geo 7×. Representative specimens of each species from each plot were systematically sampled for subsequent confirmation and/or identification in the laboratory, and the collection of the entire sampling set is kept at the herbarium of Liège University (LG). Nomenclature follows Hodgetts et al. (2020). In *Palustriella*, we distinguished, however, *P. falcata*, which occurs in the area in streams and fens, from var. *sulcata*, which is morphologically quite distinct and occurs in much drier areas. Due to the sometimes very scanty or sterile material available, identification to species level was not always possible. In the case of sibling species sharing similar niche requirements, we defined the following aggregates: *Brachythecium cirrosum* (including *B. cirrosum* s.str., *B. japygum* and *B. funkii*); *Campylium stellatum* (*C. stellatum* s.str. and *C. protensum*); *Distichium capillaceum* (*D. capillaceum* and *D. inclinatum*); *Flexitrichum flexicaule* (*F. flexicaule s.* str. and *F. gracile*); *Hymenoloma crispulum* (*H. crispulum* and *H. compactum)*; *Meesia uliginosa* (*M. uliginosa* s.str., *M. minor* and *M. minutissima*); *Mnium spinosum* (*M. spinosum* s.str. and *M. spinulosum*); *Pellia epiphylla* (*P. epiphylla* and *P. neesiana*); *Plagiomnium ellipticum* (*P. ellipticum* and *P. elatum*); *Scapania irrigua* (*S. irrigua* and *S. helvetica*); and *Weissia controversa* (*W. brachycarpa* and *W. controversa*). *Weissia*

longifolia cannot be distinguished from congeneric species when sterile, but plots located below 1400 m, wherein the species is restricted in the area, were systematically surveyed during the spring, during which *Weissia* species produce abundant sporophytes. In *Cephaloziella,* the identification of scanty or sterile material was impossible, so all specimens were assigned to 'Cephaloziella sp.'. Depauperate and/or sterile specimens of other genera that could not be determined to the level of species or aggregates where excluded from the analyses. We noted presences and absences but refrained from scoring a cover, which is challenging in Alpine bryophytes, and a frequency, which could have been assessed by counting relative occurrences among sub-plots, but which was impossible to undertake in the present survey due to time constraints associated with the large number of plots investigated.

We analysed community structure through the architecture of the species to determine whether a type of growth form of one community, regardless of taxonomic identity, could impact the composition of the other community by shaping the global structure of the canopy, thereby affecting local niche conditions, or actual interactions. Given the unavailability of continuous traits for on average 89 % of the target species in the TRY database (Kattge et al., 2020; Appendix 2), we assigned each species to one category of architectural types as defined by Barkman (1988). Barkman's system of plant architecture is a hierarchical classification based on a combination of features such as plant height, ramification pattern, leaf distribution or growth habit (Appendix 3, 4). For each plot, the importance of a given architectural type was obtained by summing-up the species of this type present in the plot. For vascular plants, for which species Braun-Blanquet cover values were recorded, we computed, for each species, the cover ratio as the ratio between its cover (Braun-blanquet classes transformed in cover ratio following Vittoz and Guisan, 2007) and the sum of covers of all other species in the

plot. For each architectural type, we then summed-up the cover ratios of all the species of this architectural type in the plot.

2.3. Environmental variables

In total, 68 variables of topography, climatic conditions, and soil conditions at a spatial resolution of 2–25 m were collected from various sources (Ginzler, 2021; Külling et al., 2024; Panchard et al., 2023) or were newly generated (see Appendix 1). We sampled the values of the environmental variables at the level of the pixel of the environmental grid that included the centroid of the biological plot. Because the environmental grid and the perimeter of the biological plots did not necessarily overlap, the centroid of the latter could, by chance, fall at the margin of a pixel of the environmental grid, raising the question of whether the conditions prevailing in the select pixel mirror those at the level of the biological plot. To address this issue, we computed the average value of the variable of interest across all 2×2 m pixels of the environmental grid that overlap with the perimeter of the target plot. We then used paired Wilcoxon tests to determine whether, on average, the value scored at the level of the 2×2 m pixel of the environmental grid that includes the centroid of the target plot differs from the average value across all pixels of the environmental grid that partly overlap with the perimeter of the target plot. Among the 22 variables at 2-m resolution, significant difference was observed only for the "Northness" with a *p*-value of 0.03, suggesting that both approaches returned similar estimates of the environmental variables prevailing in the target plot.

To account for landscape features (e.g., forest cover, glacier) surrounding the plot and that could affect conditions within it, we computed the proportion of 2.5 m resolution pixels including the target feature within a buffer zone of 25 m including the target plot. Finally, to account for the spatial structure in the data and control for spatial autocorrelation, explanatory spatial variables were derived from principal coordinates of neighbour matrices (PCNM; Borcard and Legendre, 2002; Legendre et al., 2009) using the xyz coordinates (in metres), as implemented by Paula-Souza & de Paula-Souza and Diniz Filho (2020), with the vegan R package (Oksanen et al., 2022).

2.4. Data analysis

The analyses were performed at the level of the 413 plots, for which both bryophyte and tracheophyte records were available. Hierarchical and variance partitioning was performed between the bryophyte community matrix, including all of the 281 species, and 5 predictor matrices via the rdacca.hp. package (Lai et al., 2022) in R v.4.2.2 (R Core Team, 2022). Predictor matrices included climatic variables, non-climatic environmental variables, tracheophyte community composition (320 species with >10 occurrences out of 737 species), tracheophyte community architecture, and spatial variables. The same analyses were performed to predict the composition of tracheophyte communities (737 species), using climatic and non-climatic environmental variables and composition or architectural types of bryophyte communities (< 10 occurrences, resulting in 101 out of 281 s) as predictors.

To determine whether the strength of the community composition/ environment relationship and the extent to which the factors accounting for community composition vary along the elevation gradient, all analyses were implemented along the entire elevation gradient and then successively within each of 6 elevational bands ($\leq$1000;]1000–1400;] 1400–1800;]1800–2000;]2000–2200]; > 2200), defined to get relatively similar numbers of plots across bands (62–77).

To summarise relationships among explanatory variables within each of the 5 explanatory matrices, reduce the number of predictors, and avoid multicollinearity, we used Principal Component Analyses (PCA). Instead of implementing variable selection, which sometimes lead to drastically different subsets of variables, whereas the response variable slightly varies (Guisan et al., 2002), we kept a number of axes capturing >70 % of the variance of each of the explanatory matrices. This

threshold corresponded to the maximum number of variables in the smallest dataset to stay within the limit of computation of the adjusted r^2, which corresponds to the number of plots minus 1 (Peres-Neto et al., 2006). To meet this constraint, analyses at the level of individual elevation bands were performed twice, with composition and then architecture of one lineage as predictor of the other lineage.

Hierarchical partitioning was employed to obtain the percentage of variance individually explained by each matrix (without considering the other matrix predictor) and also the variance uniquely explained by (by removing the shared effect between matrices). Variance partitioning was used to determine the exact shared effect between each matrix. To test the significance of the model, 999 random permutations of each matrix were performed and their contributions to the total explained variance were then measured and compared to the observed contribution (Lai et al., 2022).

These analyses were implemented successively using redundancy (RDA) and canonical correspondence analysis (CCA, after removing 40 and 13 plots with 0 species for bryophyte and tracheophyte matrices, respectively) to take different species response curves into account. Generalised Additive Models, which implement a nonlinear modelling framework, have also recently been implemented in variation partitioning (Gálvez et al., 2023), but could not be employed here because their implementation is currently restricted to two explanatory matrices.

3. Results

Altogether, the distribution of 281 bryophyte species was documented in 413 plots. Data is available on FigShare: https://doi.org/10.6084/m9.figshare.22778636. Tracheophyte and bryophyte species richness ranged from 0 to 102 (median = 36) and 0 to 34 (median = 8) per plot, respectively.

Along the entire elevation gradient, total variance explained of the bryophyte community composition matrix using RDA was 24 %, of which climatic conditions, other environmental variables, spatial effects, tracheophyte community architecture and composition individually contributed for 5 (*p*-value = 0.001), 13 (*p*-value = 0.001), 5 (*p*-value = 0.242), 13 (*p*-value = 0.001), and 65 % (*p*-value = 0.001), respectively. Removing shared effects, tracheophyte composition uniquely contributed to 10 % out of the 24 of the total variance explained, while climatic data and non-climatic environmental variables uniquely contributed to only 0.1 and 0.7 out of the 24 % of total variance explained (Fig. 2a). Spatial factors and tracheophyte architecture did not uniquely explain bryophyte community composition. Similar results were obtained using CCA except for the contribution of spatial effects to the total variance explained which reached 44 % (Fig. S1a, *p*-values = 0.001, 0.009, 0.375, 0.016, 0.002, for climatic conditions, other environmental variables, spatial effects, tracheophyte community architecture and composition, respectively). Total variance explained of the tracheophyte community composition matrix using RDA was 32 %, of which climatic conditions, other environmental variables, spatial effects, bryophyte community architecture and composition individually contributed for 10, 15, 29, 11 and 35 %, respectively. All *p*-values were equal to 0.001. Removing shared effects, spatial factors and bryophyte community composition were the two most important factors, uniquely accounting each for 6 of the 32 % variance explained (Fig. 2b). Similar results were obtained using CCA except that the total variance explained was only 9 % (Fig. S1b; all *p*-values = 0.001).

Total variance explained increased from <20 % below 1800 m to 35 % with RDA (Fig. 3a) and to 50 % with CCA (Fig. 3b) in bryophytes, and from <20 % to >30 % in tracheophytes with both RDA and CCA (Fig. 3c, d). For bryophytes, this increase resulted from increasing contributions of climatic and spatial factors, tracheophyte community composition and architecture (Fig. 4a, b, S2a, b). For tracheophytes, the contribution of all predictors, including climatic and abiotic, non-climatic factors, bryophytes community composition and architecture, and spatial effects, increased in alpine environments (Fig. 4 c, d, Fig. S2 c, d).
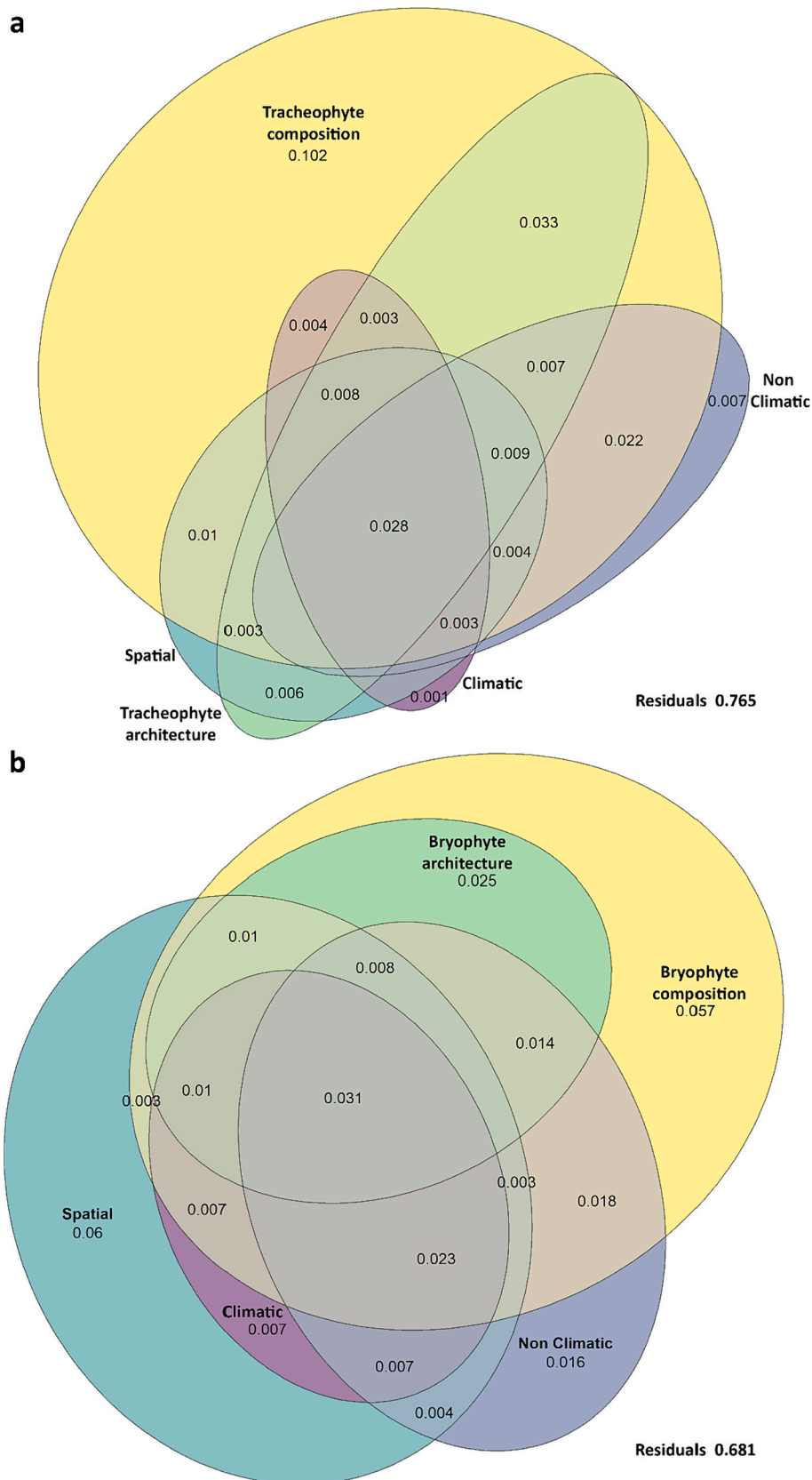
Fig. 2. Euler diagrams of the proportion of variance (numbers in ellipses) of the community composition of two lineages of land plants (bryophytes and tracheophytes) at fine spatial scale along an elevation gradient in the Western Swiss Alps explained by climatic factors, non-climatic environmental factors, spatial effects, community architecture and composition of the other lineage in a variation partitioning analysis implementing RDA (see Fig. S1 for CCA). Numbers at the level of single ellipses represent the proportion of explained variance of each variable (its unique contribution to explained variance) after removing the shared effect between matrices while numbers at the level of overlapping ellipses represent shared variance among variables.
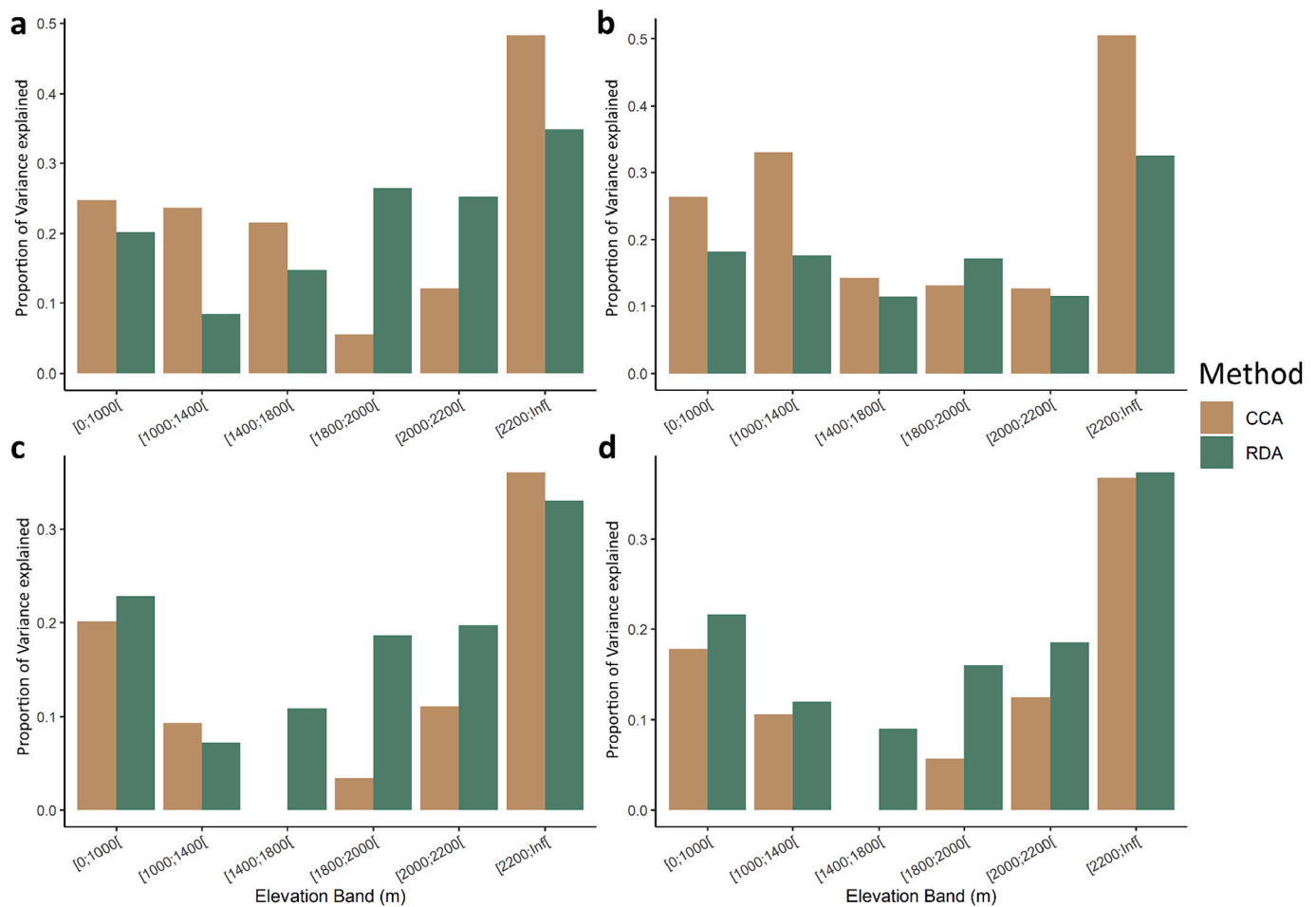
Fig. 3. Proportion of total variance of the community composition of two lineages of land plants (bryophytes [a-b] and tracheophytes [c-d]) at fine spatial scale in the Western Swiss Alps per elevation band explained by climatic factors, non-climatic environmental factors (Nclim), spatial effects, and community composition [a-c] or architecture [b-d] of the other lineage in a hierarchical partitioning analysis implementing either RDA or CCA.

a. Tracheophytes explaining bryophytes. b. Bryophytes explaining tracheophytes. in b, due to negative values in the interactions between several matrices, the unique contribution of climatic and bryophyte architecture was impossible to show (0.005 and 0.004, respectively). Negative values are not shown.

4. Discussion

Climatic variation at 25-m resolution was a significant predictor of bryophyte and tracheophyte community composition along the entire elevation gradient, but climatic data contributed less than other environmental variables, accounting for 5 and 10 % of the total variance explained of the bryophyte and tracheophyte community composition matrices, respectively. The relatively minor role played by climatic variation contrasts with the primary role played by climatic variation in analyses of spatial patterns in tracheophyte species distributions across the Alps at 1-km resolution (Chauvier et al., 2021). This suggests that, despite the large differences in climatic conditions at 600 and 3000 m, other abiotic and biotic factors play an increasingly important role as resolution increases (Gazol and Ibáñez, 2010; Laliberté et al., 2009; Lewis et al., 2014; Pearson and Dawson, 2003). This is particularly true in alpine environments, wherein seasonal mean temperatures can differ by 8 K among plant species assemblages growing in the close vicinity of each other at the same elevation (Körner et al., 2023; Körner and Hiltbrunner, 2021). Nevertheless, climatic variation at 25 m resolution contributed twice more to the total variance explained in tracheophyte than in bryophyte communities, suggesting that the former, due to their

small size and occurrence under the herb canopy, are even more decoupled from local climate conditions at 2 m above ground than the latter.

Non-climatic environmental factors alone added another 13 % and 15 % of explained variance in bryophyte and tracheophyte species composition along the entire gradient, respectively. In tracheophytes. Bergauer et al. (2022) similarly reported that, at the scale of 10 m² plots scattered along an elevation gradient of >1000 m, topography, amount of litter and herb cover prevailed over climatic conditions in explaining variation in bryophyte species richness. While it becomes evident that increasing the resolution of analyses aiming at assessing climate change impact on species distributions is necessary (Lembrechts, 2023; Maclean and Early, 2023), such a shift of scale also involves the implementation of a large number of non-climatic predictors, in line with growing evidence that the entire ecological space needs to be considered when modelling species distributions and community composition (Collart et al., 2023; Mod et al., 2016; de Oliveira et al., 2021; Scherrer and Guisan, 2019; Tessarolo et al., 2021).

The remaining explained variance was partitioned between spatial effects and the contribution of community composition and architecture of one lineage to the community composition of the other lineage. Spatial factors were not significant for bryophytes in the analyses implementing RDA but individually accounted for 29 % of the variation explained for tracheophytes. Disentangling the role of deterministic, ecological factors from spatial processes has commonly been used as a mean to contrast the application of niche vs neutral theories in ecology (see Viana et al., 2022 and references therein). It is at first sight tempting
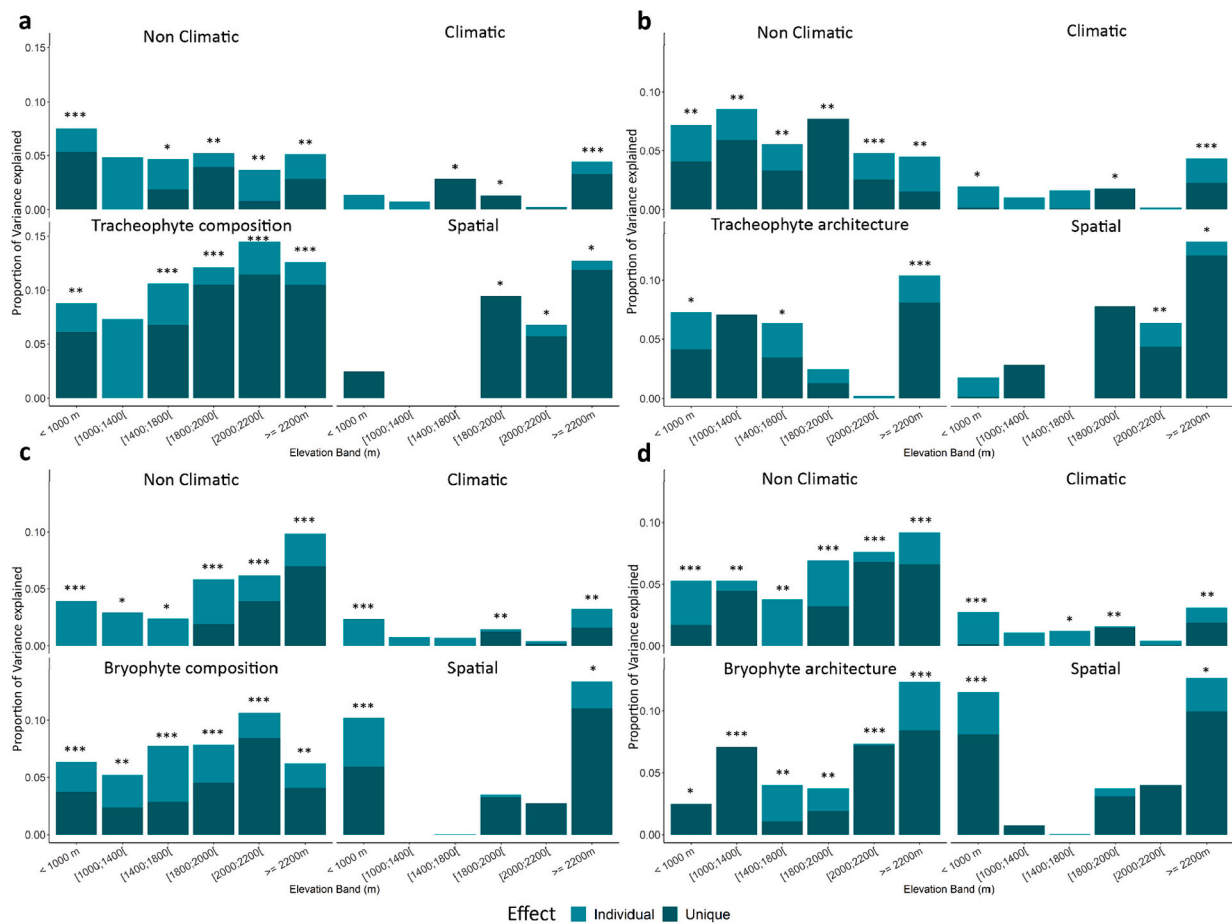
Fig. 4. Hierarchical partitioning implementing RDA (see Fig. S2 for results with CCA) of the factors accounting for community composition of two lineages of land plants (bryophytes [a-b] and tracheophytes [c-d]) at fine spatial scale in the Western Swiss Alps. Factors include climatic factors, non-climatic environmental factors, spatial effects, and community composition or architecture of the other lineage. Bars represent the proportion of variance individually and uniquely explained by each factor. ***: p-value = 0.001; **: p-value <0.01; *: p-value <0.05.

to interpret the prevalence of abiotic factors over spatial effects in bryophytes in terms of the more important role of niche availability as compared to dispersal limitations in such efficient dispersers (Cacciatori et al., 2020). Likewise, the striking difference of the importance of spatial effects between bryophytes and tracheophytes mirrors the higher dispersal capacities of the former thanks to their very small, airborne spores (10–30 μm) and vegetative propagules that can travel across very long distances, as shown by experimental (Barbé et al., 2016; Lönnell et al., 2012; Sundberg et al., 2006), genetic (see Vanderpoorten et al., 2019 and references therein) and phylogeographic (see Patiño and Vanderpoorten, 2018 for review) evidence. Nevertheless, the importance of spatial factors was very different when implementing RDA or CCA in the variation partitioning analyses. In fact, the spatial component in variation partitioning analyses must be interpreted with extreme caution, as it does not only reflect differences in the strength of the processes of interest, but also the influence of the unique spatial arrangement of the environmental variables in each system, which cannot be disentangled (Gilbert and Bennett, 2010; Smith and Lundholm, 2010).

The use of tracheophyte species composition as a predictor of bryophytes species composition allowed for a substantial increase of explained variance, contributing to no <32–61 % of the latter depending on the analyses. Schaffers et al. (2008) similarly reported that plant community composition consistently outperformed environmental conditions in predicting arthropod assemblages. Plant community composition reflects and synthesises the habitat conditions across a number of causal factors and could be interpreted in terms of

unmeasured (hidden) abiotic factors and direct interactions between the tracheophyte and bryophyte layers. 'Hidden' factors may include a series of factors of contemporary land-use, such as livestock density (Fragnière et al., 2022), as well as past land-use and environmental conditions (Lewis et al., 2014), which may have left an imprint in current patterns of community composition, even in organisms with high dispersal capacities such as bryophytes and lichens (Ellis and Coppins, 2009, but see Hutsemékers et al., 2023).

'Hidden' factors may also include the same variables as the ones included in the present study, but at finer resolution. Although the necessity of using highly resolved predictors to explain and predict plant species distributions, especially in mountain environments, was emphasised (Chauvier et al., 2022), it is unclear whether higher-resolution climate data (e.g., Lembrechts et al., 2019; Stark and Fridley, 2022) and topographic data up to 1 m (Chytrý et al., 2024; Pradervand et al., 2014) necessarily improve the accuracy of species distribution models. Topographic variables at coarser resolution (>20 m) may even better predict vascular plant species distributions than higher-resolution variables because of 'spatial mass effects', according to which, to harbour a large and viable population of a species, a site must include a sufficient number of suitable micro-habitats (Chytrý et al., 2024). We suggest that, at least for small-sized organisms like bryophytes that rely on microhabitat conditions, microtopography, microclimatic variables and light intensity at even finer scales, would be crucial. In these conditions, local climates such as those investigated here do not reflect the near-surface climatic conditions that are experienced by small organisms (Pincebourde et al., 2016). By their small

stature and high foliage density, alpine plants in particular engineer a microclimate that differs greatly from free air and what taller species experience (Körner, 2021).

Disentangling the role of such hidden factors from that of direct interactions between bryophytes and tracheophytes is challenging. After removing shared effects, variation in architectural types of the herb canopy did, however, not contribute to bryophyte community composition, tending to suggest that direct canopy effects played a comparatively lower role than other interactions such as the effect of tracheophyte species on the soil chemistry and texture at the microscale and 'hidden' environmental variation. While the impact of tracheophyte architecture on the composition of the bryophyte community has been well-documented (Bates, 1988), we interpret its somewhat mitigated effect here along the entire elevation gradient in terms of a trade-off between the positive effects of the herb layer at mid-densities, which may generate a buffered microclimate favourable for the bryophyte layer (Ingerpuu et al., 2005), and competitive effects for light and space under dense herb canopies (van der Wal et al., 2005; Zechmeister et al., 2003; Jaszczuk et al., 2023). In fact, the impact of herb canopy architecture was much more evident within elevation belts, and especially, in alpine conditions, where facilitation seems to prevail (see below).

Tracheophyte community composition explained about twice more bryophyte community composition than the reverse. This suggests, as expected, that tracheophytes exert a stronger nursing effect on bryophytes than the reverse (but see Lett et al., 2018 and Gavini et al., 2019), but also, potentially, that tracheophytes are better predictors of local environmental conditions than bryophytes. While tracheophyte indicator values showed significant correlations with in-situ measurements of soil conditions (Descombes et al., 2020 and references therein) and were shown to improve species distribution models (Scherrer and Guisan, 2019), it would be extremely interesting to compare the latter with bryophyte indicator values, which have been most recently updated (van Zuijlen et al., 2023).

Altogether, using a comprehensive set of environmental predictors (climatic and non-climatic) and vegetation architecture to predict bryophyte and tracheophyte community composition along an elevation gradient, we found that 24 % of the variation in bryophyte community composition was captured by a combination of environmental predictors and tracheophyte composition and architecture, while 32 % of the variation in tracheophyte community composition was captured by a combination of environmental predictors and bryophyte composition and architecture. This proportion alone is, however, not easy to interpret. While percentages of variance explained are comparable among similar data, using the same set of explanatory variables, such as nested data from a common dataset, these proportions can hardly be directly compared to other studies. The unexplained proportion in fact reflects unmeasured environmental variables, but also complex spatial relationships, which may vary from one study to another, stochasticity in biological processes (e.g., dispersal, mortality), and lack-of-fit of data to the response model (Økland, 1999). Here, the percentage variance explained are globally in line with those reported in regional datasets at resolutions of a few metres (e.g., 4 % in Singh et al., 2019; 10 %, Hokkanen, 2006; 13 %, Táborská et al., 2020; 22 %, Staniaszek-Kik et al., 2019; 45 %, French et al., 2008 and Ilić et al., 2023).

Most importantly, the percent explained variance substantially varied across the elevation gradient, underlining the fact that the strength of the species composition-environment relationship varies depending on environmental conditions themselves (Paula-Souza & de Paula-Souza and Diniz Filho, 2020). Total variance explained increased towards high elevation, from a minimum of 7 % of total explained variance at low elevation up to 50 % above 2200 m. In tracheophytes, an increase of the contribution of non-climatic environmental factors was observed at high elevation, in line with the hypothesis of a stronger environmental control under harsher conditions in alpine environments (Gálvez et al., 2023; Leibold and Chase, 2017; Myers et al., 2013; Souffreau et al., 2015). The relative increase of the total variance explained towards high

elevation belts was associated with spatial effects and vegetation architecture, both in terms of tracheophyte architecture contributing to bryophyte community composition and of bryophyte architecture contributing to tracheophyte community composition. In fact, bryophyte and tracheophyte species tend to be more similar in size in alpine environments than at lower elevation. Plants above the treeline are small 'by design' as a result of the selection of dwarf phenotypes adapted to the alpine environment, and bryophyte and tracheophyte communities contribute to generate densely packed vegetation favouring facilitation (Choler et al., 2001; Körner et al., 2023), wherein 'benefactor' species (Odling-Smee et al., 1996) modify habitats and allow beneficiary species to co-occur (Kikvidze et al., 2005). In their review on interactions within plant communities, Soliveres and Maestre (2014) reported that the importance of positive interactions peaks in alpine areas, wherein over 25 % of the species are more spatially associated with nurse plants than expected by chance, leading to aggregated distribution patterns. In particular, cushion plants have typically been identified as 'benefactor' species whose distinctive growth form can function as a heat, moisture and nutrient trap (see Kjær et al., 2018, and references therein, but see Liancourt and Doležal, 2023). This is particularly true for bryophytes, wherein moderately dense stands are dehydrated less rapidly than loose stands or isolated shoots because a dense packing of shoots may reduce water loss by effectively reducing the diameter of capillary spaces among close neighbours. Hence, shoot size, biomass production and species diversity are often positively related to carpet density (Bergamini et al., 2001).

5. Conclusion and perspectives

In the context of mounting evidence for the need of shifting to finer scale in biodiversity studies to take environmental, and especially, climatic conditions actually experienced by organisms into account (Lembrechts, 2023), comprehensive environmental data at 25-m resolution have become increasingly available (Haesen et al., 2021; Külling et al., 2024). Our results suggest that, despite the availability of a comprehensive set of abiotic variables at 2–25 m resolution, these data still insufficiently account for variation in plant species composition at fine resolution. Ongoing efforts to generate high resolution data of soil and near-surface temperature worldwide (Lembrechts et al., 2020) offer a promising perspective for improvement. Modelling high-resolution climate data will require, however, a series of complementary predictors. In particular, microtopography, which can now be derived at extremely fine resolution using drones (Duffy et al., 2021) or LiDAR technologies (Shukla et al., 2023), can capture temperature differences of large elevational (or latitudinal) gradients over very short horizontal distances (Scherrer and Körner, 2010) and may be used to establish the relationship between macro- and microclimatic variation (Gril et al., 2023) to enhance our ability to predict species distributions under present and future conditions.

CRediT authorship contribution statement

Flavien Collart: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas Kiebacher:** Writing – review & editing, Data curation. **Marion Quetsch:** Writing – review & editing, Resources. **Olivier Broennimann:** Writing – review & editing, Resources. **Antoine Guisan:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Alain Vanderpoorten:** Writing – review & editing, Writing – original draft,

Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available on FigShare: https://doi.org/10.6084/m9.figshare.22778636.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171741.

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